A Novel Hybrid *Polypodium* (Polypodiaceae) from Arizona

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Abstract.—A previously unrecognized interspecific hybrid in the fern genus *Polypodium* is described from collections made at a single remote locality in central Arizona. Originally identified as *P. glycyrrhiza*, this sterile nothotaxon is easily distinguished from other members of the genus and is here named *Polypodium* ×*aztecum* Windham & Yatsk. The hybrid is tetraploid, exhibiting ca 37 bivalents and 74 univalents at diakinesis. Based on geographic proximity and shared morphological traits, we conclude that *P. hesperium* is one of the parents of the new taxon. Assuming that the hybrid is more or less intermediate between *P. hesperium* and a second parental taxon, we attempt to identify the missing parent. The most likely candidate is *P. calirhiza*, a species of Oregon, California, and Mexico that has not been documented from Arizona. However, we cannot rule out the possibility that the missing parent is an as yet unidentified member of the *P. plesiosorum* complex from Mexico.

In January, 1979, a biologist for the U.S. Forest Service encountered an unusual colony of *Polypodium* growing in a remote canyon of the Sierra Ancha in Gila County, Arizona. A sample comprising a piece of rhizome and a few withered fronds was submitted to Arizona State University for identification. The collection was examined by Timothy Reeves, then a doctoral student working on pteridophytes at the ASU herbarium. No doubt impressed by the large size of the mostly free-veined fronds and the intensely sweet flavor of the rhizomes, Reeves (1981) reported the find as the first Arizona record of *Polypodium glycyrrhiza* D.C. Eat. This report was noted by Lellinger (1985) in his guide to pteridophytes of the United States and Canada.

During floristic research for the Vascular Plants of Arizona project, we had occasion to examine the original collection at ASU. A number of morphological differences were noted between the Arizona specimen and typical plants of *P. glycyrrhiza*, including the fact that the spores (and often the sori) of the Arizona plant were malformed and apparently nonfunctional. We revisited the Gila County locality in 1981 and 1982 to obtain samples for biosystematic analyses, which revealed that the colony represented a sterile tetraploid deviating from the description of *P. glycyrrhiza* in a number of ways (Windham, 1985). Based upon the findings of Windham (1985), Haufler *et al.* (1993) excluded Arizona from the distribution of *P. glycyrrhiza*, but did not speculate on the true identity of the plant in question.

As detailed below, the Arizona plant represents a sterile hybrid. Because this taxon is morphologically distinct from all other members of the Polypodiaceae

known to occur in the southwestern United States, we have assigned it the following binomial:

Polypodium ×*aztecum* Windham & Yatsk., *hybr. nov.* Type.—U.S.A., Arizona, Gila County, Sierra Ancha, SE wall of Devil's Chasm at a point 3.02 km ENE of the summit of Aztec Peak, elev. 4500 ft, August 7, 1981, *Windham, Yatskievych & Hevly 283* (holotype: ASC; isotypes: ARIZ, IND, MEXU, MICH, MO, NY, UC, US, UT). Paratype: same locality, 10 Jan 1979, *Warner s.n.* (ASU). Fig. 1.

Hybrida ex origine incerta; differt a P. hesperio rhizomatibus intense dulcibus, frondibus grandioribus (usque ad 50 cm longis et 12 cm latis), pinnis medianis plerumque longoribus quam 3 cm, costis adaxialibus puberulentibus, sporangiis pilis bicellularibus glandulosis, et sporis (plerumque sporangiis) abnormalibus et abortivis.

Rhizomes 4–9 mm in diameter, widely creeping, branched, firm, green turning dark brown with age, infrequently somewhat pruinose, intensely sweet flavored, paleaceous; *rhizome scales* mostly 4–6 mm long, 30–60 cells wide near the point of attachment, lanceolate-ovate, tapered symmetrically to a deciduous capillary tip, denticulate near the apex, deeply cordate with overlapping basal lobes, tan to brown, rarely with indurated cells forming a poorly defined darker median stripe. *Leaves* relatively closely spaced along the rhizome, erect or strongly ascending; *petiole* 2–15 cm long, shorter than the lamina, green to brownish stramineous, with scattered inconspicuous multicellular glands; *lamina* (5–)15–31 cm long, (3–)6–12 cm wide (1.6–3.3 times as long as wide), oblong-ovate to narrowly deltoid in outline, widest near the base, pinnatisect with 8–34 lateral pinnae and a somewhat attenuate pinnatifid apex, herbaceous to subcoriaceous, both surfaces puberulent with scattered inconspicuous multicellular glandular trichomes, abaxial surface and rachis with occasional linear-lanceolate scales (2–7 cells wide); *pinnae* mostly alternate, 1–6 cm long, 0.4–1.5 cm wide (2.5–5.5 times as long as wide), narrowly oblong, tips rounded to narrowly acute, margins finely serrulate, especially distally, costa sparsely and minutely puberulent adaxially; *hydathodes* opposite the sori on the adaxial pinna surface, large, oval, many-celled; *veins* free or very rarely anastomosing near the margin, forking 1–4 times, terminating submarginally, with thickened tips, usually evident in mature leaves; *sori* oval, located medially between costa and pinna margin at the tip of each lowermost vein branch; *sporangiasters* absent; *sporangia* mostly abortive, with bicellular glands on the surface, annular cells usually poorly developed; *spores* abnormal, and abortive, the size, shape, and number per sporangium highly variable. $2n =$ ca 148 (ca. 37 II + 74 I; counted from the holotype).

GEOGRAPHY AND ECOLOGY OF THE TYPE LOCALITY

Located in Gila County in central Arizona, the Sierra Ancha is a topographically and geologically complex mountain range. Most of the range lies within
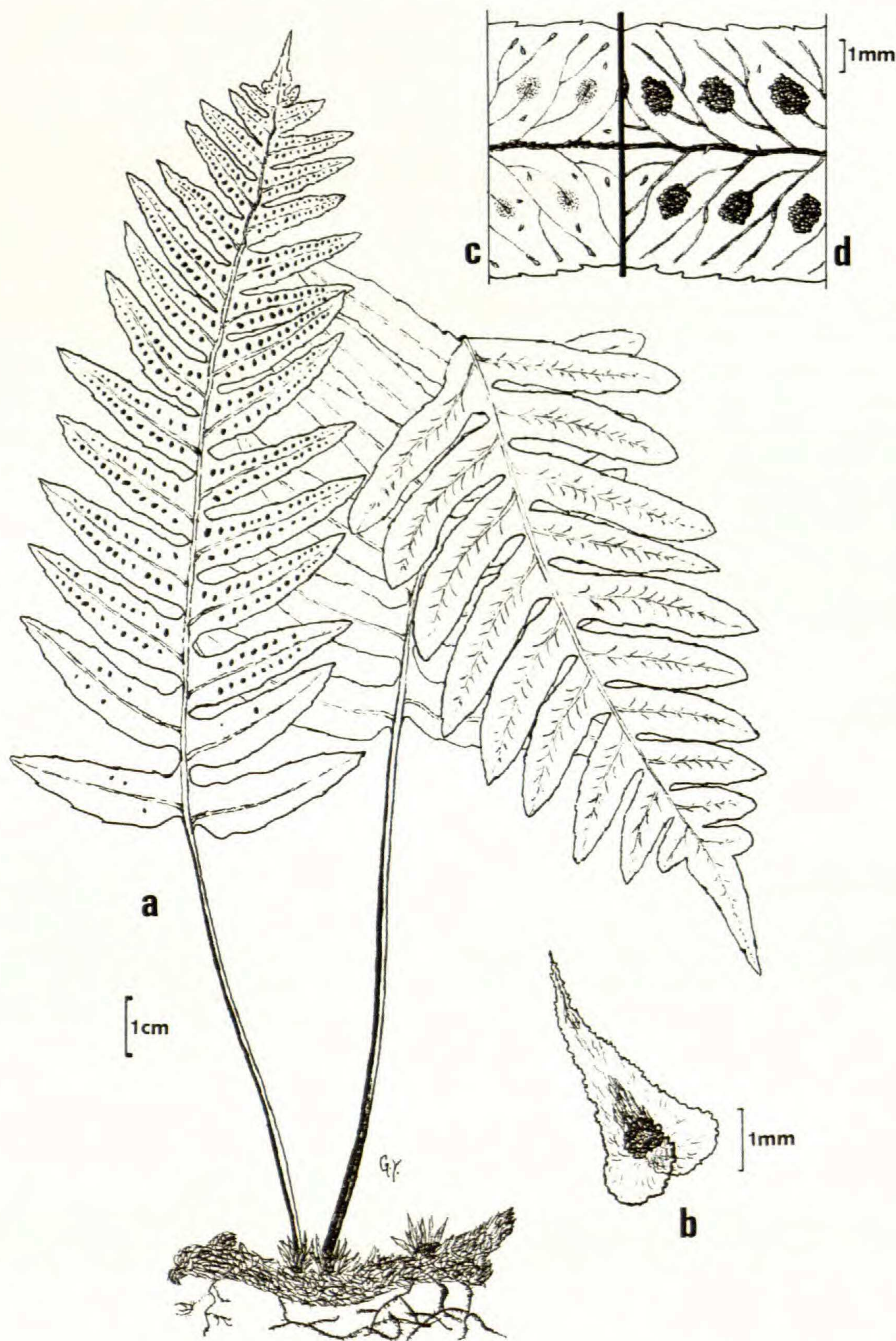
FIG. 1.   *Polypodium × aztecum.* A) habit; B) rhizome scale; C) adaxial pinna surface; D) abaxial pinna surface.

the boundaries of Tonto National Forest, and the southeastern portion, including the type locality of *P. ×aztecum*, is part of the Sierra Ancha Wilderness. The mountain range trends from northwest to southeast, with numerous drainages running southwestward and northeastward from its spine. Aztec Peak, a prominent landmark toward the southern end of the range, is the highest point, with an elevation of 2345 m (ca. 7700 ft). *Polypodium ×aztecum* occurs in Devil's Chasm, one of the northeastward-flowing drainages originating near Aztec Peak. From its mouth at ca. 975 m along Cherry Creek, this rugged gorge ascends roughly 1000 m over a course of about 5 air km. The geology of the canyon is extremely diverse, with different stretches of the drainage exhibiting outcrops of granite, travertine, quartzite, sandstone, and conglomerate.

Polypodium ×aztecum is known from a single colony occurring in the narrowest part of Devil's Chasm at an elevation of ca. 1350 m. At this location, the canyon transects the Dripping Springs Formation, a Precambrian quartzite highly resistant to erosion. The result is a precipitous gorge nearly 100 m deep and just 10 m wide at the bottom. Prone to recurrent flash-flooding, these narrows support little vegetation in the canyon bottom proper.

Polypodium ×aztecum occurs on a north-facing slope approximately 5 m from the streambed. The colony, which appears to represent a single genetic individual, covers an area of nearly 5 × 10 m. Rhizomes form a dense mat in areas where soil has accumulated, with individual branches extending into cracks and crevices of adjacent quartzite ledges. The soil, largely derived *in situ* from the quartzite bedrock, is rich in organic matter. Because of the depth and orientation of the canyon, the site rarely receives direct sunlight. Thus, although stream flow is intermittent in this section of the drainage, the fern occupies a relatively moist microhabitat.

Surrounding vegetation is transitional between deciduous riparian woodland (Interior Southwestern Riparian Deciduous Woodland, *sensu* Brown, 1982) and a more xeric-adapted evergreen woodland. Immediate associates include *Celtis*, *Clematis*, *Morus*, *Galium*, and *Opuntia*. Nearby slopes support species of *Quercus*, *Pinus*, *Ceanothus*, *Cercocarpus*, *Nolina*, and *Agave*. The canyon is rich in fern species, especially below the Dripping Springs Quartzite where stream flow is permanent. However, the only other fern found in the immediate vicinity of the Aztec polypody is the closely related *P. hesperium* Maxon.

CYTOLOGY OF THE HYBRID

Samples for cytological analysis were collected both in the field and from material brought into cultivation. Developing sporangia (for meiotic counts) and actively growing root tips (for mitotic counts) were fixed and examined using standard chromosome squash techniques (see Windham, 1985). Unfortunately, *Polypodium ×aztecum* proved to be a difficult subject for cytological analysis. Mitotic preparations were hard to score because of the large number of chromosomes and the tendency of chromosomes to clump together in spite of repeated careful squash preparations. Nevertheless, the better preparations seemed to show 148 chromosomes.
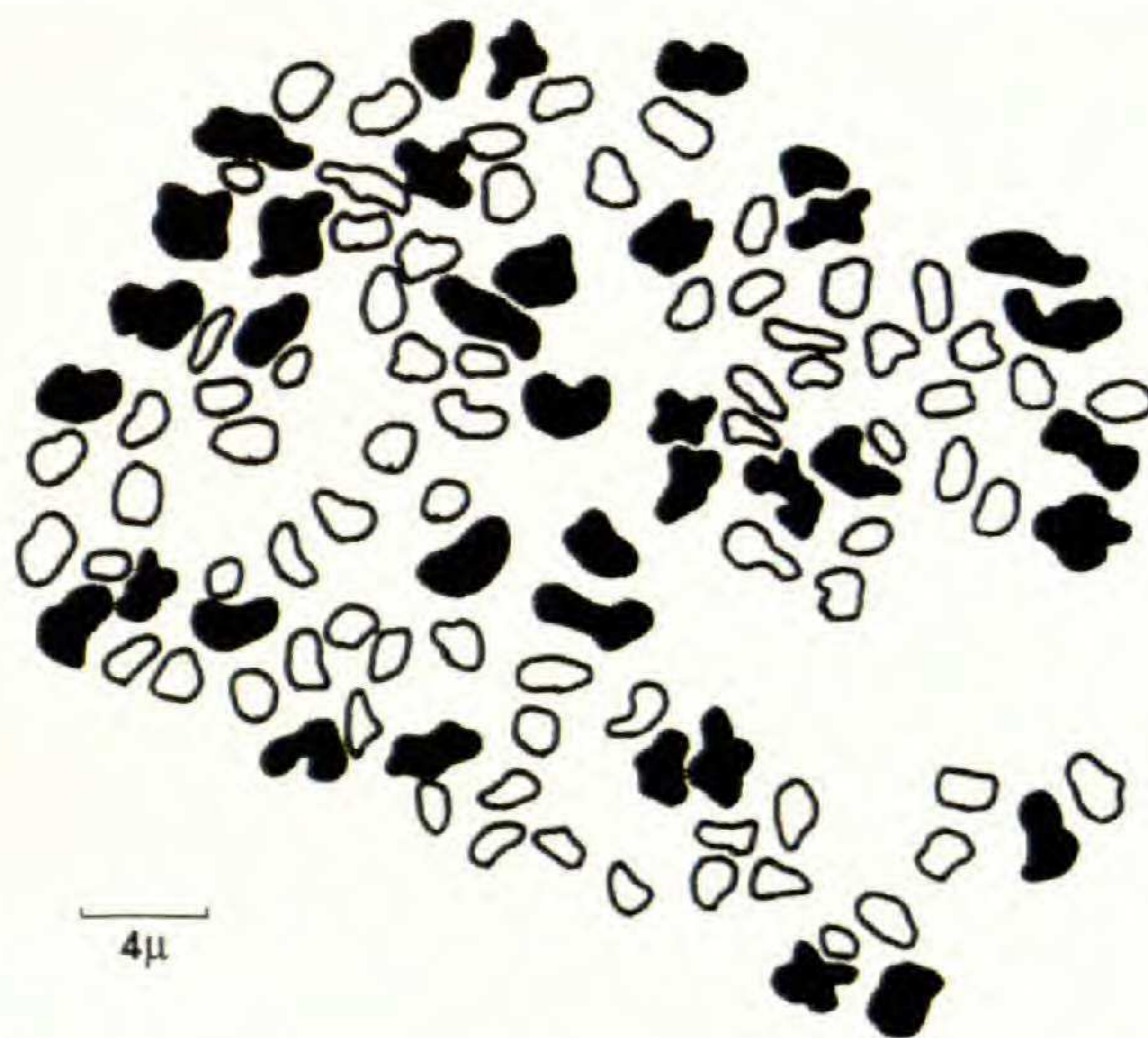
FIG. 2.   Diakinesis in *Polypodium* ×*aztecum*. Camera lucida drawing of cell showing ca. 37 bivalents (solid) and 74 univalents (outlined).

It soon became apparent that most sporangia in this taxon abort prior to the spore mother cells undergoing meiosis. Additionally, in those sporangia that matured sufficiently to provide dividing cells, the chromosomes stained poorly and were sometimes difficult to distinguish from the cytoplasm. From the few cells that could be scored in meiotic preparations, 111 total chromosomes were visible. Cells at diakinesis appeared to contain approximately 37 bivalents and 74 univalents (Fig. 2). Minor uncertainty is attributable to the fact that large univalents are sometimes difficult to distinguish from bivalents, as has been noted in several other fern hybrids (e.g., Wagner and Wagner, 1976). The observation of about 148 units at anaphase confirmed that *P.* ×*aztecum* is a tetraploid. The wholesale abortion of spores (in those sporangia surviving to the spore production stage) apparently is attributable to irregularities in chromosome pairing at meiosis and indicates that this taxon is incapable of sexual reproduction.

ORIGIN OF THE HYBRID

Interspecific hybrids are very common among ferns (Wagner, 1969; Werth *et al.*, 1985; Barrington *et al.*, 1989), and it generally is a simple matter to establish the parentage of a sterile hybrid when both parents are found in close proximity. The process becomes more difficult when only one related species is known to occur within a 500 km radius of the hybrid. Given the complete sexual sterility of *P.* ×*aztecum*, we conclude that it must have been formed *in situ* in Devil's Chasm. As the only other member of *Polypodium* to occur in the vicinity, *P. hesperium* must have played a role in its origin. Substantial morphological differences between these taxa (Table 1) indicate that *P. hesperium* is not the sole progenitor of *P.* ×*aztecum*. However, the apparent

TABLE 1. Hypothesized features of the "missing parent" of *Polypodium* ×*aztecum* based on the assumption that the hybrid is more or less intermediate between its putative parents.

Characters/Taxa	P. hesperium	P. ×aztecum	"Missing parent"
Rhizome taste	Acrid or sweet	Sweet	Sweet
Rhizome scale coloration	Rarely slightly bicolorous	Overwhelmingly concolorous	Concolorous
Leaf dissection	Pinnatifid	Pinnatifid	Pinnatifid
Abaxial rachis scales	Linear-lanceolate	Linear-lanceolate	Linear-lanceolate
Blade texture	Herbaceous to subcoriaceous	Herbaceous to subcoriaceous	Herbaceous to subcoriaceous
Length of medial pinnae	To 3 cm	To 6 cm	At least 5 cm
Adaxial costae	Glabrous	Sparsely puberulent	Puberulent
Arrangement of sori on each side of costae	Single row	Single row	Single row
Leaf venation	Free	Very rarely anastomosing	Sporadically anastomosing
Sporangiasters	Absent or very rare	Absent	Absent
Sporangial pubescence	Absent or unicellular	Bicellular	Multicellular
Ploidy level	Tetraploid	Tetraploid	Tetraploid

absence of any other species of *Polypodium sensu stricto* in the Sierra Ancha (or in the whole of Arizona) complicates efforts to identify the other parent.

The failure to find a second parent in or near the hybrid colony is somewhat unusual, but two possible explanations can be offered. On the one hand, sporophytic plants of the missing parent may have existed in Devil's Chasm in the past but failed to persist in the area. Alternatively, *P.* ×*aztecum* could represent a case of long-distance hybridization, initiated by the chance dispersal of a foreign *Polypodium* spore into the local *P. hesperium* population. In either case, the density and areal coverage of rhizomes in the colony suggest that these events occurred hundreds of years ago.

Without geographic proximity to guide our selection of potential parents, we must depend heavily on morphology and cytology to narrow the field of potential candidates. Hybrid ferns typically exhibit character states either intermediate or incompletely additive between their parents (Wagner, 1969; Werth and Lellinger, 1992). If we assume this generalization to be true in the case of *P.* ×*aztecum* and further assume that *P. hesperium* is one of its parents, it becomes possible to predict some of the distinguishing features of the missing parent. These predictions are based on two underlying principles: 1) that traits shared by the known parent and the hybrid should appear relatively unchanged in the unknown parent, and 2) that the unknown parent should show more extreme expressions in characters that distinguish the hybrid from the known parent. These principles are well established in the study of fern hybrids and provide the basis for describing presumably extinct species (such as *Dryopteris* "semicristata"; see Wagner et al., 1969; Kuhn and Werth, 1990) whose only genetic legacy is the allopolyploids they produced in the remote past (Werth and Lellinger, 1992).

Based on the assumptions and principles outlined above, we attempted to

reconstruct the salient features of the missing parent of *P.* ×*aztecum*. This analysis, encompassing most of the characters used to distinguish *Polypodium* species in the *Flora of North America* (Haufler *et al.*, 1993), is presented in Table 1. From this, we predict that the unknown parental species should have a sweet rhizome covered with concolorous rhizome scales. It would have pinnatifid leaves with widely scattered, linear-lanceolate scales on the abaxial surface of the rachises, and blades that are herbaceous to subcoriaceous in texture. The largest medial pinnae should be at least 5 cm long, with puberulent adaxial costae, a single row of sori on each side of the costae, and sporadically anastomosing venation. Sporangiasters would be absent, but the sporangia should have a few multicellular hairs. Finally, because both *P.* ×*aztecum* and *P. hesperium* are tetraploid, the missing parent should also occur at this ploidy level.

In addition to *P. hesperium*, Haufler *et al.* (1993) list ten other species of *Polypodium sensu stricto* as occurring in North America north of Mexico. Based on our hypothetical description of the unknown parent of *P.* ×*aztecum*, most of these are easily eliminated from consideration. *Polypodium triseriale* Swartz, a tropical epiphyte with clathrate rhizome scales, fully pinnate leaves, strongly anastomosing venation, and 2–3 rows of sori on each side of the costae, is only distantly related to other North American polypodies (Haufler *et al.*, 1993) and clearly could not be involved in the origin of the Arizona hybrid. The strictly coastal *P. scouleri* Hook. & Grev., with its stiff, leathery fronds, regularly anastomosing venation, and glabrous costae and sporangia, also is a poor candidate for the missing parent. The entire *P. virginianum* L. complex (including *P. amorphum* Suksdorf, *P. appalachianum* Haufler & Windham, *P. saximontanum* Windham, *P. sibiricum* Sipliv., and *P. virginianum*) can be excluded from consideration as well. All of these species have acrid rhizomes with mostly bicolorous scales, lanceolate-ovate rachis scales, pinnae less (usually much less) than 4.5 cm long, glabrous costae, free venation, and usually abundant sporangiasters.

The three remaining species of *Polypodium* occurring north of Mexico constitute the *P. glycyrrhiza* complex (Lloyd and Lang, 1964; Haufler *et al.*, 1995). As traditionally defined, this complex includes *P. californicum* Kaulfuss, *P. glycyrrhiza*, and the allotetraploid derived from hybridization between them, *P. calirhiza* S.A. Whitmore & A.R. Sm. *Polypodium californicum*, with its acrid to bland rhizomes, deltate to ovate abaxial rachis scales, more regularly anastomosing venation, glabrous sporangia, and diploid chromosome number, is very unlikely to be the missing parent of *P.* ×*aztecum*. *Polypodium glycyrrhiza* is a closer match, as might be expected given Reeves' (1981) initial identification of the hybrid. However, this species deviates from our hypothetical description of the unknown parent in its linear (hairlike) abaxial rachis scales, strictly free venation, glabrous sporangia, and uniformly diploid chromosome number. Thus, *P. glycyrrhiza* is neither the correct identification of the Arizona plant nor the missing parent of it.

The only member of the *P. glycyrrhiza* complex with a chromosome number matching that of the hypothetical missing parent is the allotetraploid *P. calirhiza*. This species also has the right combination of genomes to explain

the meiotic pairing behavior observed in *P.* ×*aztecum*. Isozyme studies by Haufler *et al.* (1995) have confirmed earlier hypotheses (Lloyd and Lang, 1964; Whitmore and Smith, 1991) that *P. calirrhiza* contains the genomes of *P. californicum* and *P. glycyrrhiza. Polypodium hesperium*, the known parent of *P.* ×*aztecum*, also is an allotetraploid, produced by hybridization between *P. amorphum* and *P. glycyrrhiza* (Haufler *et al.*, 1995). A hybrid between *P. hesperium* and *P. calirhiza* thus would contain four sets of chromosomes derived from three different parental diploids. Two of these chromosome sets come from *P. glycyrrhiza*, and they should pair to form 37 bivalents during the first division of meiosis (see Shivas, 1961). *Polypodium amorphum* and *P. californicum* are more distantly related (Haufler *et al.*, 1995), and we would expect the chromosomes derived from these species to remain unpaired, producing 74 univalents. Therefore, a hybrid between *P. hesperium* and *P. calirhiza* should show ca. 37 II + 74 I at meiosis I, exactly the situation observed in *P.* ×*aztecum* (Fig. 2).

The similarities between *P. calirhiza* and the missing parent of *P.* ×*aztecum* extend far beyond cytology, encompassing most of the morphological features in our hypothetical description (Table 1). In fact, *P. calirhiza* appears to deviate from our predictions in just two characters: rhizome taste and sporangial pubescence. Given the intensely sweet taste of *P.* ×*aztecum* rhizomes, we would predict that those of the unknown parent would be similarly sweet. However, the rhizomes of *P. calirhiza* typically are described as acrid, though with an underlying sweetness (Whitmore and Smith, 1991; Whitmore, 1993). Our prediction that the sporangia of the missing parent should be pubescent with oligocellular hairs also is not met in *P. calirhiza*, which has only glabrous sporangia. Though seeming to disqualify *P. calirhiza* as the unknown parent of *P.* ×*aztecum*, both of these characters require additional scrutiny.

The original diagnosis of *P. calirhiza* states that the rhizome is "dulcibus et acerbis" (Whitmore and Smith, 1991: 236), but we have found considerable variation in this trait. Some populations produce rhizomes that are intensely sweet with little hint of bitterness, whereas the rhizomes in other populations are definitely acrid (Windham, unpubl. data). The same situation is encountered in *P. hesperium* (Table 1), another allopolyploid arising through hybridization between *P. glycyrrhiza* and a species with acrid rhizomes. In both *P. calirhiza* and *P. hesperium*, half the genetic program codes for sweet rhizomes and the other half for acrid. The variability observed in these taxa suggests that this 50/50 combination can produce individual plants spanning the entire range from intensely sweet (*glycyrrhiza*-like) to acrid. A hybrid between *P. hesperium* and *P. calirhiza*, which would contain two chromosome sets from *P. glycyrrhiza* and one each from *P. amorphum* and *P. californicum*, would carry a similar 50/50 mix of genes coding for rhizome taste. Such a hybrid could fall out anywhere on the spectrum between intensely sweet and acrid. Thus, we cannot eliminate *P. calirhiza* as the missing parent of *P.* ×*aztecum* on the basis of rhizome taste.

Sporangial pubescence provides the only real challenge to the involvement of *P. calirhiza* in the origin of *P.* ×*aztecum*. No *Polypodium* species included in the *Flora of North America* consistently has pubescent sporangia (Windham,

unpubl. data). In fact, the only taxon in the region to express this trait at all is *P. hesperium*, which occasionally shows a few, unicellular glands on the sporangial capsules (Table 1). Like the variability in rhizome taste discussed above, the sporadic appearance of sporangial pubescence in this allopolyploid species probably results from the interaction of disparate genetic programs derived from its diploid progenitors (Haufler *et al.*, 1995). As indicated previously, *P. hesperium* originated through hybridization between *P. glycyrrhiza* (which lacks sporangiasters) and *P. amorphum* (which has sporangiasters with unicellular glands). Although their function is not entirely clear, sporangiasters appear to be homologous with sporangia (Kott and Britton, 1982). Thus, taxa combining genomes from species lacking sporangiasters and species with pubescent sporangiasters occasionally may express an intermediate character state: pubescent sporangia.

Although the foregoing suggests that it is possible to produce pubescent sporangia through hybridization among North American species of *Polypodium*, it may not be an adequate explanation for the situation encountered in *P. ×aztecum*. If *P. calirhiza* were the missing parent of *P. ×aztecum*, then the hybrid would contain three chromosome sets (two from *P. glycyrrhiza* and one from *P. californicum*) coding for no sporangiasters and one (from *P. amorphum*) coding for sporangiasters with unicellular glands. Based on the precedent set by *P. hesperium*, we would expect this combination to yield an even more sporadic occurrence of sporangia with unicellular glands. This seems an unlikely origin for the distinctive, bicellular glands observed on the sporangia of *P. ×aztecum*. Though it is impossible to gauge the genetic and taxonomic significance of this trait, it would be preferable if the taxon proposed as the missing parent of *P. ×aztecum* matched all aspects of our hypothetical description. This requires that we expand our search beyond the region covered by the *Flora of North America*.

Although pubescent sporangia are rarely observed among north temperate representatives of *Polypodium*, they are common among subtropical Mexican taxa and often are used to distinguish species (Smith, 1981). In fact, most of the character states mentioned in the hypothetical description of the missing parent occur in one or more species of the Mexican *P. plesiosorum* Kunze group, which is thought to provide a link between temperate and tropical elements of the genus (Tryon and Tryon, 1982). Unfortunately, we are unable to identify a likely candidate for the unknown parent of *P. ×aztecum* among these species due to a lack of critical information. The North American fascination with rhizome taste has not extended to Mexico, and we cannot say which, if any, members of the *P. plesiosorum* alliance have the sweet rhizomes characteristic of the missing parent. Also, cytogenetic data are lacking for many species, making it impossible to determine which potential prospects have the necessary tetraploid chromosome number.

The identity of the unknown parent of *P. ×aztecum* presents an interesting dilemma. We can argue that *P. calirhiza* is the mystery taxon, downplaying the lack of sporangial pubescence and citing the near-perfect match in all other characters. Or, we can hold out for an unidentified Mexican species that might

agree perfectly with the hypothetical description if only sufficient information were available. We had hoped to resolve this dilemma through molecular analyses, but were unable to extract DNA from the available herbarium specimens. The senior author revisited the type locality of *P. ×aztecum* in August, 2000 to assess the status of the colony. In the process, he discovered that a devastating wildfire had swept through large portions of Devil's Chasm, incinerating much of the vegetation in the canyon. There was no active growth of *P. ×aztecum* foliage, and most of the rhizome mat had been destroyed. However, under the shelter of a large *Opuntia*, several rhizome branches remained alive. It is hoped that the colony, probably the only one of its kind, will recover in time and that we will once again have the opportunity to study this remarkable fern. But for now, the exact parentage of *P. ×aztecum* remains a mystery.

The answers to questions surrounding the origin of this novel hybrid must await more intensive studies using molecular and other biosystematic data. Because its parentage remains uncertain, we are unable to apply a formula name, as is often done in the case of rare hybrids (e.g., *Polypodium calirhiza ×scouleri*). Therefore, we have chosen to propose a formal binomial, which does not seem unreasonable given that *P. ×aztecum* is so distinct from other polypodies present in the southwestern United States. Giving the taxon a formal name facilitates discussion by systematists, floristicians, conservationists, and land managers and, hopefully, will contribute to the recognition and survival of this unique hybrid.

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